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Personal perspective

A study on the dynamic features of photosystem stoichiometry: Accomplishments and problems for future studies

Yoshihiko Fujita
Department of Marine Bioscience, Fukui Prefectural University, Obama, Fukui 917, Japan

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Abstract

Our study on the regulation by light of photosystem stoichiometry in cyanophytes is briefly reviewed here. It can be summarized as follows: Adjustment of photosystem stoichiometry results in optimization of photosynthetic efficiency under the prevailing light-growth conditions. Photosystem (PS) I is primarily affected, increasing or decreasing, relative to PS II. The regulation of PS I synthesis appears to be at the translation or the post-translational level. The regulation is probably governed by changes in the redox level of the electron transport components, most probably at Cyt b_6 in the Cyt b_6–f complex. Our results to date are at the physiological level, but they have raised many questions and provided suggestions for future directions in exploring the mechanism of regulation, some of which are discussed in this perspective.

Abbreviations: APC – allophycocyanin; CAP – chloramphenicol; Chl – chlorophyll; ETS – electron transport system; HQNO – 2-heptyl-4-hydroxyquinoline *N*-oxide; LHC II – light-harvesting complex for Photosystem II; PBS – phycobilisome; PC – phycocyanin; PE – phycoerythrin; Pchlide – protochlorophyllide; PQ – plastoquinone Q_c; PQ – reduction site of Cyt b_6–f; Q_z – PQH_2 oxidation site of Cyt b_6–f

Introduction

Almost 40 years ago, I first became involved in the study of complementary chromatic adaptation of cyanophytes. Our studies with *Tolypothrix tenuis* confirmed the initial observations made many years ago (Engelmann 1883, 1902; Gaidukov 1903) by showing that the quality of the light, under which the cells were grown, determined which phycobiliprotein predominated (Hattori and Fujita 1959; Fujita and Hattori 1960). Cells grown in red light produced mostly phycocyanin (PC) while cells in green light produced the complementary pigment, i.e. phycoerythrin (PE). At the same time, another type of adaptation to the light quality was found by the two foremost research groups in photosynthesis, those of Blinks and of Emerson. In red algae they found that the quantum yield of photosynthesis under PE-absorbed light varied with light quality. The yield was higher in cells grown under the light absorbed by PE than in those grown under the light absorbing chlorophyll *a* (Chl *a*), irrespective of the PE/Chl *a* ratio (Yocum and Blinks 1958; Brody and Emerson 1959). Later, Jones and Myers (1964) found the same phenomenon in the cyanophyte *Anacystis nidulans* Tx20, where the proportion of PC to Chl *a* varied significantly when grown under light absorbed by PC vs. Chl *a* (cf. Figure 1). The feature is very different from complementary chromatic adaptation that we studied at that time. Since then, we have been wondering how the quantum yield is regulated in the adaptation of this type.

In 1980, Myers et al. (1980) found that the stoichiometry of two photosystems in *Anacystis nidulans* Tx20 varied depending on the light regime for cell growth. The stoichiometry of Photosystem I (PS I) to Photosystem II (PS II) was greater than one in cells

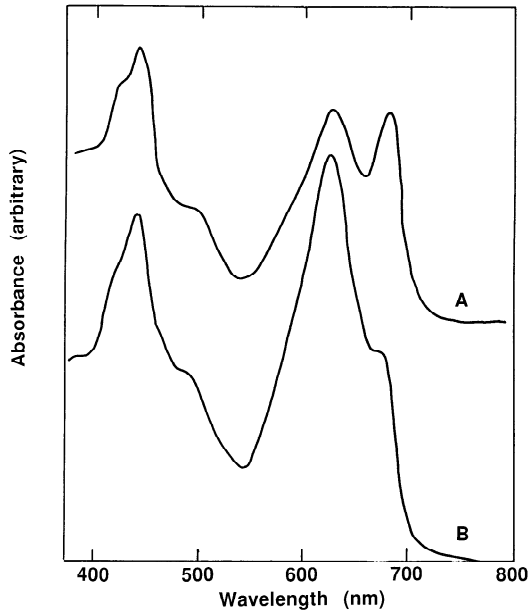

Figure 1. Absorption spectra of intact cells of *Synechocystis* PCC6714 grown under colored light absorbed mainly by PBS (PS II light; A) and that absorbed preferentially by Chl *a* (PS I light; B). The figure in Murakami (1996) is reproduced by courtesy of the author.

grown under white fluorescent light that was absorbed mainly by phycobilisome (PBS) while the stoichiometry was almost one in cells grown under red light that was absorbed by Chl *a*. At about the same time, we found that light intensity caused changes in the stoichiometry (Kawamura et al. 1979). Thus, in subsequent studies when we examined variation of the stoichiometry in several cyanophytes and the red alga *Porphyridium cruentum* we used weak chromatic light so as to minimize any intensity effects. Our examination (Fujita et al. 1985) confirmed that variation of the stoichiometry observed by Myers et al. (1980) was ascribable to light quality and suggested that the stoichiometry change improved photosynthetic efficiency. Similarly, Manodori and Melis (1986) confirmed stoichiometric effects caused by light quality in *Anacystis nidulans* Tx20. Our examination (1985) also showed that during the stoichiometry change, PBS/PS II ratio remained almost constant in cyanophytes. Our observation suggesting that the variation of photosystem stoichiometry changes the photosynthetic efficiency and the pigmentation like those in the adaptation of photosynthetic efficiency observed by Yocum and Blinks (1958), by Brody and Emerson (1959) and by Jones and Myers (1964) led us to assume that the adaptation might be the same phenomenon as the variation of photosystem stoichiometry induced by the light quality.

Stoichiometric changes dependent on light quality and light intensity were also found in vascular plants (Table 1, see also Anderson 1986). The collective results from other various laboratories led us to conclude that the photosystem stoichiometry is not constant and depends on the light-growth conditions.

Many questions arose, and we asked: How might the photosynthetic efficiency be improved with changing photosystem stoichiometry? Are both photosystems affected? We have tried to resolve some of these questions in the past ten years, however, much remains as yet unsolved. Followings are summary of our previous results and the problems remaining for the future.

A summary of previous studies

PS I is responsible for variation of the PS I/PS II ratio

We determined abundance of PS I, PS II and Cyt b_6–f complexes in cells of *Synechocystis* PCC6714 grown under various conditions. As seen in Table 2 the stoichiometry of PS I to PS II varied markedly depending on light quality, but the ratio of PS II to Cyt b_6–f remained fairly constant. Furthermore, the PBS amount , as indicated by PC and APC, relative to PS II was also constant under autotrophic conditions. The stoichiometry in cells that were heterotrophically grown was almost the same as that in cells grown under PS II light. From these results we concluded that the variable component responsible to the variation of photosystem stoichiometry is PS I (Fujita and Murakami 1987). Later, the same results were also obtained with *Synechocystis* PCC6803 (Aizawa et al. 1992). Based on such results we proposed the hypothesis that the variation is induced in response to redox state of the electron pool between the two photosystems (Fujita et al. 1987).

Adjustment of PS I/PS II ratio improves photosynthetic efficiency

Previous observations on variation of the quantum yield under different light regimes (Yocum and Blinks 1958; Brody and Emerson 1959) led us to assume that the variation of photosystem stoichiometry resulted in enhanced photosynthetic efficiency. We confirmed this idea by experiments where we showed that the overall photosynthetic efficiency improved in cells that

Table 1. PS I/PS II ratio in chloroplasts of vascular plants grown under various light regimes

Plant	PS I/PS II ratio		Reference
I White light	Low intensity	High intensity	
Pisum sativum	1.0	0.4	1
	0.8	0.6	2
Sinapis alba	1.5	1.0	3
II Colored light	PS II light[a]	PS I light[a]	
Arabidopsis thalina	0.6	0.4	4
Asplenium auslasium	0.5	0.2	5
Hordeum vulgare	0.7	0.4	6
Lycopersicon esculentum	0.5	0.3	7
Pisum sativum	1.0	0.5	8
	0.9	0.4	9
Spinacia oleracea	0.7	0.5	10
Tradescantia albiflora	0.5	0.4	11

[a] Colored lights mainly absorbed by respective photosystems.
Reference: 1, Leong and Anderson (1986); 2, Chow and Anderson (1987); 3, Wild et al. (1986); 4, Walters and Horton (1994); 5, Leong et al. (1985); 6, Kim et al. (1993); 7, Smith et al. (1993); 8, Glick et al. (1986); 9, Chow et al. (1990), 10, Chow et al. (1991); 11, Liu et al. (1993). For the effect of colored light, data reported recently are also included.

Table 2. Stoichiometric relationship among thylakoid components in cells of *Synechocystis* PCC6714 grown under various conditions

Growth conditions	Content relative to PS II				
	PC	Allophycocyanin (APC)	Chl *a*	Cyt b_6–f	PS I
	[monomer mol(mol PS II)$^{-1}$]			[mol(mol PS II)$^{-1}$]	
Autotrophic, under					
PS I light	138	33	198	0.87	1.16
PS II light	132	30	453	0.91	3.02
Heterotrophic, with glucose	104	30	359	0.88	2.16

Abundance of PS II was fairly contant among three types of cell. The ratio of abundance in autotrophic cells under PS I light, in cells under PS II light and in heterotrophic cells was 1.00:0.83:0.92. Recalculated from data in Fujita and Murakami (1987).

had adjusted their PS I/PS II ratio to the light regime (Murakami and Fujita 1988). Melis et al. (1989) independently came to the same conclusion from their studies with *Anacystis nidulans* Tx 20. Also, analysis of flash-induced oxidation-reduction reactions of Cyt*f* and P700 (Murakami and Fujita 1991a) revealed that the variation of the stoichiometry improved the photosynthetic efficiency releasing the redox state of the electron pool between two photosystems from the state biased by the shift of light quality. The same occurred in variation of the stoichiometry in response to light intensity (Murakami and Fujita 1991b). The improvement of the photosynthetic efficiency by the adjustment

of photosystem stoichiometry was also reported with vascular plants (Chow et al. 1990; Kim et al. 1993).

Identification of ETS component monitored for variation of the stoichiometry

Whereas we initially assumed that the redox state of plastoquinone (PQ) pool might be monitored like in 'state transitions' (cf. Williams and Allen 1987; Fujita et al. 1994), but we found this was not confirmed by the behavior of Cyt *f* . A rapid reduction of flash-oxidized Cyt *f* was always found under the conditions that induced the increase in the abundance of PS I (Murakami and Fujita 1991a). The reduction is far faster than the reduction by PQH_2 in PQ pool suggesting that the Cyt *f* reduction depended on the Q cycle of Cyt b_6–*f* . Later, we found that the rapid reduction was suppressed by HQNO, which suppresses the Q cycle of Cyt b_6–*f* in this organism (Matsuura et al. 1988). Although HQNO suppressed the increase of PS I, it did not effect the decrease of PS I under PS I light (Murakami and Fujita 1993). From such results, we hypothesized that the redox level of Cyt b_6 is monitored through the HQNO-sensitive oxidation reaction of the cytochrome probably at the Q_c site of Cyt b_6–*f* complex. The reaction may reduce some unknown component. The reduced level of the component may be the primary signal and transduced to induce the synthesis of PS I; higher signal level may cause the increase in PS I resulting in a higher PS I/PS II stoichiometry.

Identification of the step(s) controlling the synthesis of PS I complex

Inhibition experiments with chloramphenicol (CAP) suggested that changes in photosystem stoichiometry occurred only under biosynthetic conditions, i.e. synthesis of PS I (Fujita et al. 1988). We examined the dynamics of photosystems with pulse-labeling and pulse-chase experiments (Aizawa and Fujita 1992, 1997). Results summarized in Table 3 indicate that (1) the synthesis of either photosystem complex is far more rapid than its degradation, and (2) the rate of synthesis of PS I (monitored by PsaA/B polypeptides) is variable; the rate was twice as rapid under the light regime that induced a high PS I/PS II stoichiometry (PS II light) than the rate under the light regime that induced a low stoichiometry (PS I light). Acceleration and deceleration of synthesis were completed within 30 min after changes in the light regime ($T_{1/2}$, 10 to 20 min for the acceleration under PS II light and 3 to 5 min for the deceleration under PS I light). Thus, we concluded that regulation of synthesis, and not degradation, of PS I complex was a primary cause for the variation of the photosystem stoichiometry.

We first considered that regulatory point may be at the transcriptional level. However, this is unlikely since *psaA/B* mRNA level is not altered by the light quality (Aizawa and Fujita 1997). We also found an anomalous effect of the inhibitor for peptide elongation on the synthesis of PsaA/B polypeptides. At low concentration of the inhibitor, the synthesis was insensitive to, or even stimulated by, the inhibitor, while the synthesis of total proteins was suppressed normally (Table 4; Aizawa and Fujita 1997). Such anomalous effect of the inhibitor was more marked in the slower synthesis under PS I light. The inhibition pattern suggests that the synthesis is regulated at the step(s) other than peptide elongation, the initiation of translation or at another level which involves the insertion of Chl *a* into the apoproteins. Differential appearance of the effect under two light regimes also suggests that the step(s) is suppressed under PS I light and released from the suppression under PS II light. It has been shown that decreased synthesis of Chl *a* selectively reduced the synthesis of PS I (Fujita et al. 1990). Light quality may alter the synthesis of Chl *a* at the protochlorophyllide (Pchlide) photoreduction step. In fact, the reduction was greater under PS II light than that under PS I light (Fujita et al. 1995). However, we found that the Pchlide photoreduction did not limit the synthesis of PS I under our experimental conditions (Fujita et al. 1995; Aizawa and Fujita 1997).

Hypothetical model for the variation of photosystem stoichiometry

From the above mentioned results, we have proposed a model to explain how the variation of photosystem stoichiometry may come about (Figure 2). The model is drawn under presumption that the photosystem stoichiometry varies solely with the regulation of the synthesis of PS I, and thus, explains the relationship between the synthesis of PS I (represented by the synthesis of PsaA/B polypeptides) and the ETS state. In cells of low PS I/PS II ratio, the electron pool between the two photosystems, such as PQ and Cyt b_6–*f*, is highly reduced after shift to PS II light (Fujita et al. 1987; Murakami and Fujita 1991a). Under such electron transport state, a rapid and HQNO-sensitive Cyt *f* reduction becomes marked (Murakami and Fujita

Table 3. Synthesis and degradation of PsaA/B and PsbA polypeptides in cells of *Synechocystis* PCC6714 under PS I light and PS II light

Photosystem polypeptides	Rate of synthesis[a] under		Degradation[b] under	
	PS I light	PS II light	PS I light	PS II light
PsbA	1.00	1.09	19	5
PsbC	1.00 (1.22)	1.16	17	14
PsaA/B	1.00 (0.90)	2.03	15	7
Total proteins	1.00 (44.7)	1.03	–	–

[a] Rates determined by pulse-labeling with ^{35}S methionine are expressed as relative to those under PS I light. Numbers in parentheses are isotope incorporations into respective protein fractions relative to that into PsbA.
[b] Decrease in the isotope amount (%) during 96-min chase.
(Data from Aizawa and Fujita 1997.)

Table 4. The effect of CAP on the synthesis of PsaA/B polypeptides and total proteins in cells of *Synechocystis* PCC6714 under PS I light and PS II light

Concentration of CAP (μM)	Synthesis of			
	PsaA/B under		Total proteins under	
	PS I light	PS II light	PS I light	PS II light
0	100	100	100	100
0.3	121	105	96	98
0.6	113	105	91	93
1.2	97	87	81	78
4.0	44	31	33	44

Rates of synthesis of respective proteins were determined by pulse-labeling with ^{35}S-methionine in the presence of CAP at respective concentrations. Values relative to those without CAP are presented (recalculated from data in Aizawa and Fujita 1997).

1991a). Since HQNO also inhibited the increase of PS I under PS II light (Murakami and Fujita 1993), we assume that HQNO-sensitive Cyt b_6 oxidation is the primary reaction for the signal to induce the synthesis of PS I. The reaction may occur at the Q_c site of Cyt b_6–f . The primary component of signal transduction system (A in Figure 2) may be activated through its reduction coupling with Cyt b_6 oxidation, or PQH_2 formed at the Q_c site may activate A. We assume that the active A thus formed induces synthesis of PS I through unknown signal transduction system (dotted open arrow in Figure 2). We do not know the nature of the signal transduction system, but it is possible that the system is 'two-component system' type.

As noted above, we interpret the anomalous CAP effect as that the synthesis of PS I is regulated at the translational or the post-translational level (open arrow in Figure 2). The step(s) may be arrested (block sign in Figure 2) unless the signal from Cyt b_6 oxidation releases the step(s) from the arrested state or activates the step. The increase in the synthesis of PS I may result in a higher PS I/PS II ratio and cancel the over-reduced state of the electron pool between two photosystems (cf. Murakami and Fujita 1991a). Then, the signal from Cyt b_6 oxidation may become smaller, and the synthesis of PS I may become slower and balanced with that of PS II to maintain a constant and proper PS I/PS II ratio. In cells of high PS I/PS II ratio, the signal from Cyt b_6 oxidation may be insignificant under PS I light, and thus, the synthesis of PS I may be arrested until the signal becomes significant.

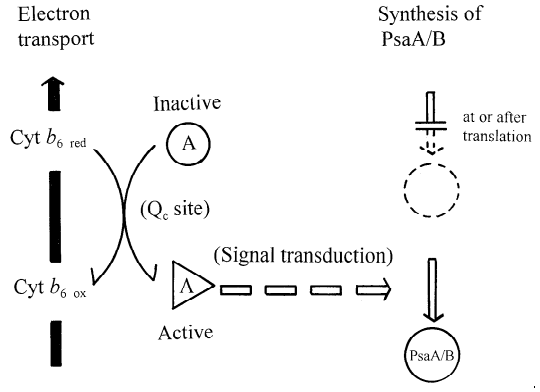

Figure 2. A hypothetical model for the regulation of PS I synthesis represented by the synthesis of PsaA/B polypeptides *in Synechocystis* PCC6714. A, unknown component sensing the redox level of Cyt b_6 (enclosed by circle, inactive; by triangle, active); solid arrow; direction of electron flow; dotted open arrow, signal transducing system; open arrow; the process of PsaA/B synthesis. Details, see the text.

Cells of *Synechocystis* PCC6714 grown heterotrophically in the dark showed a high PS I/PS II ratio like in cells grown under PS II light (Fujita et al. 1987; Fujita and Murakami 1987). The model in Figure 2 can also explain a high PS I/PS II ratio in such cells. The respiratory electron flow in thylakoids of this organism appears to be limited at the step of Cyt *c* oxidase (Fujita et al. 1987). Thus, Cyt *f* is fully reduced, and the rapid and HQNO-sensitive Cyt *f* reduction is significant even after PS I/PS II ratio has attained to a high level (Murakami and Fujita 1991a). According to the model, the signal from Cyt b_6 oxidation is always significant under the dark heterotrophic conditions resulting in a high PS I/PS II ratio.

Revaluation of our hypothetical model and problems for future study

Most of our studies have remained at the physiological level, thus leaving many questions for a full interpretation of our model. Some of them concern the mechanism of the reactions, and others, a validity of our model. The section following deals with important questions raised by our model.

Do both photosystems vary simultaneously?

Our results indicated that active response to light quality and light intensity affected an increase of PS I in *Synechocystis* PCC6714. The same type of response was observed with *Synechocystis* PCC6803 (Aizawa et al. 1992) and *Synechococcus* PCC6301 for light quality (Matsuura and Fujita 1986) and *Anabaena variabilis* for light intensity (Kawamura et al. 1979). We found the same response to light quality in the green alga *Chlamydomonas reinhardtii* also (Melis et al. 1996). The evidence indicating an active response of PS I abundance to light intensity was reported with pea (Leong and Anderson 1986). Thus, we have thought that the variation of PS I is a common pattern in the regulation of photosystem stoichiometry.

Not all algae respond the same way as those noted above. In the red alga *Porphyridium cruentum* (Cunnigham et al. 1990) and *Porphyra yezoensis* (Abe et al. 1993), both PS I and PS II change independently when grown under different light quality (Table 5). Furthermore, such an adjustment was also observed with the marine cyanophyte *Synechococcus* NIBB 1071 (Table 5; Abe et al. 1993), thus it is not simply a difference between prokaryotes and eukaryotes. Interestingly we also found a positive correlation in the number of PS II/PBS in species in which only PS I is variable. For example, in *Synechocystis* PCC6714 the stoichiometry between PS II and PBS is unity and this organism only adjust PS I in response to changing light regimes.

Thus, the following question arises: Is the abundance of PS II in red algae and in the marine *Synechococcus* actively regulated, and if so, does the regulation occur in the synthesis or by degradation? It is likely that the photodamage of D1 in PS IIcomplex is more marked under PS II light than that under PS I light (cf. Kim et al. 1993) resulting in a significant decrease in PS II under PS II light. A careful re-examination of data for *Synechocystis* PCC6714 suggests that although almost insignificant, the stoichiometry between PS II and Cyt b_6–*f* tends to be smaller in cells grown under PS II light. Further, we observed that PS I/PS II ratio under PS II light was, in most cases, slightly higher than double of the ratio under PS I light whereas PS II light enhanced the synthesis of PsaA/B polypeptides at most double. PS II may be degraded differentially under two light regimes, and such degradation of PS II may somewhat emphasize the difference in PS I/PS II ratios in the two types of cells. However, if degradation of PS II occurs, it must be so slow as to be undetected by our pulse-chase experiment for a short time.

Table 5. Changes in the PS II content in response to light quality observed with the red alga *Porphyra yezoensis* and the marine cyanophyte *Synechococcus* NIBB1071

Organism	Light regime for cell growth	PS II	Cyt b_6–f	PS I
		[mol(mol monomer APC)$^{-1}$]		
Porphyra yezoensis				
	PS I light	3.5	1.8	2.5
	PS II light	1.6	1.7	9.5
Synechococcus NIBB1071				
	PS I light	12.0	7.2	15.6
	PS II light	6.6	7.2	21.0

Abundance of components are expressed as that on a per ACP basis. ACP is contained at a constant amount in PBS, so that the values correspond to those on a per PBS basis (from Abe et al. 1993).

What is the target of light regulation?

We first considered that the redox level of the PQ pool could be responsible for the regulation, analogous to 'state transitions' in green plants (cf. Williams and Allen 1987; Fujita et al. 1994). However, analysis of the flash-induced oxidation-reduction of Cyt *f* and the effect of HQNO did not support this and suggested that the redox level of Cyt b_6 or the electron flux through Cyt b_6 is involved with the regulation. The latter can also explain the regulation corresponding to the light intensity (Murakami and Fujita 1991b). However, we have to assume a speculative component for sensing Cyt b_6 oxidation (A in Figure 2). Despite of its importance in our hypothesis, we have no evidence as yet of the nature of the component. Recently, Verner et al. (1997) reported that PQH_2 at the Q_Z site of Cyt b_6–f , but not free PQH_2 in PQ pool, was associated with the activation of protein kinase for LHC II phosphorylation in 'state transitions' of the vascular plant spinach. The site of Cyt b_6–f to be monitored is different from our hypothesis for the regulation of photosystem stoichiometry. Does such discrepancy come from phylogenetic level of organisms tested? Is the sensing mechanism different from each other? Answers of these important questions await for the identification of the speculative component in our hypothesis.

Also to be solved is the nature of the signal transduction. As described above, we observed kinetic difference between the acceleration and the deceleration of PS I synthesis (Aizawa and Fujita 1992, 1997) which could suggest that the signal transduction is rate-limited by the different enzymes in the processes of acceleration and deceleration. This evidence led us to suspect that 'two-component type mechanism' is functional in the light regulation. Analysis with mutants that are impaired in the ability to adjust the photosystem stoichiometry may be most powerful to solve this problem. We searched for such mutants, but our attempts in finding such mutants has not been as yet successful.

In the first paper of our study on the regulation of photosystem stoichiometry (Fujita et al. 1985), we supposed that the regulation arises in response to changes in the proportion between non-cyclic electron flow (NADPH and ATP production) and cyclic one (ATP production). Simultaneously, Melis et al. (1985) independently proposed a similar hypothesis where the PS I/PS II stoichiometry was thought to be regulated by the ratio of NADPH/ATP. Although we have not determined the ratio yet, I suspect that the ratio before the acclimation of the photosystem stoichiometry will correlate with the variation of the stoichiometry; when the ratio of NADPH to ATP becomes higher upon the shift of light regime may occur the variation to a higher photosystem stoichiometry. It may be possible that the imbalance of the ratio is monitored through thioredoxin system like the activation of the translation of *psbA* mRNA in *Chlamydomonas* (cf. Levings III and Siedow 1995). The idea that the ratio of NADPH to ATP is monitored for the regulation of photosystem stoichiometry is still alive as far as our model remains speculative.

Which step in the synthesis of PS I is controlled?

Our tentative conclusion is that synthesis of core polypeptides of PS I (PsaA/B polypeptides) is regulated at the translation or the post-translation level. Firstly, we found that the level of *psaA/B* mRNA active for translation is not significantly different between cells grown under two types of light suggesting that tran-

scription and processing of transcripts are probably not regulated. Secondly, the differential inhibition of PsaA/B synthesis with CAP was more marked under PS I light than under PS II light. Noteworthy is that CAP at low concentration elevated the rate of PsaA/B synthesis (Table 4). We repeated the experiment and confirmed the stimulating effect. How was the rate of the synthesis elevated?.

We measured the increase in **stable** PsaA/B polypeptides for determining the synthesis of PS I complex (cf. Aizawa and Fujita 1997). Our experiments with the mutant of *Plectonema boryanum* that lacked Pchlide dark reductase indicated that Chl *a* molecules are essential for the synthesis of **stable** PsaA/B polypeptides. Thus, our results did not necessarily indicate the synthesis of nascent polypeptides. The effect of CAP suggested that some step(s) other than peptide elongation was regulated. Together with the effect of CAP, Chl *a*-dependent synthesis of **stable** polypeptides suggests that insertion of Chl *a* is regulated suppressively under PS I light. However, we do not know details of mechanism for Chl *a* insertion into polypeptides. Elucidation of such mechanism may be necessary for evaluating a possibility that regulation occurs in the process of insertion of Chl *a*. Alternatively, differential effect of CAP on the synthesis of PsaA/B polypeptides under two light regimes may provide a key for the analysis of the mechanism for insertion of Chl *a*. Another possible step(s) for the regulation may be the initiation of translation. If it is correct, some special component(s), possibly proteinous, may be needed for the formation of mRNA-ribosome complex, like formation of *psbA* mRNA-ribosome complex (cf. Leving III and Siedow 1995).

We have only examined the dynamics of PsaA/B polypeptides thus far, but not other polypeptides, but wonder what mechanisms coordinate the synthesis of the numerous polypeptides of a PS I complex and ask if shared regulatory steps are involved.

What is the regulatory role of ETS in thylakoids?

As for thylakoid system, several regulatory phenomena occur responding to the redox state of the electron pool between two photosystems. The 'state transitions', the regulation of photosystem stoichiometry and the *cab* gene expression (Escoubas 1995; Maxwell et al. 1995) are such examples. Although interpretation of signal-monitoring mechanism is not necessarily the same, I suspect that they share a common signal-monitoring mechanism and that such mechanism acts as a central tool for regulating thylakoid electron transport to maintain the efficiency of energy conversion.

Table 6. Simultaneous variation of the electron turnover capacity of PS I and Cyt *c* oxidase in cells of *Synechocystis* PCC6714 under under various stress-conditions

Conditions	PS I/PS II	Cyt *c* oxidase activity[a]
Under PS I light		
Normal[b]	1.64	0.72
Plus 0.5 M NaCl	2.13	–
Minus CO_2, plus 3 mM HCO_2^-	2.79	1.08
Under PS II light		
Normal[b]	2.61	1.56
Plus 0.5 M NaCl	3.92	2.03
Minus CO_2, plus 3 mM HCO_3^-	3.39	2.18

[a] Cyt *c* activity (Vmax) on a per Cyt b_6–*f* basis is presented [10^3mol O_2 uptake (mol Cyt b_6–*f*)$^{-1}$ h^{-1}].
[b] Cells were grown in standard medium (modified MDM; cf. Gu et al. 1994) with continuous supply of 5% CO_2.
Data in Gu et al.(1994) and in Murakami et al. (1997a) are presented after recalculation.

Respiratory O_2 uptake by intact cells of *Synechocystis* PCC6714 was found to vary in parallel with the variation of PS I abundance (Adhikary et al. 1990). Since the respiratory electron transport appears to be limited at the terminal Cyt *c* oxidase step in this organism (Fujita et al. 1987), the possibility exists that regulation occurs at the activity of this enzyme in parallel with the regulation of photosystem stoichiometry. Gu et al. (1994) confirmed the validity of this assumption by determining the activity of Cyt *c* oxidase in cells grown under different light regimes. We found a parallel regulation of the abundance of PS I and the activity of Cyt *c* oxidase in response not only to the light regime, but also to environmental stresses which modified the state of ETS (high NaCl, low CO_2) (Table 6; Murakami et al. 1997a). A parallel variation of electron turnover capacity of the two terminals of thylakoid ETS, PS I and Cyt *c* oxidase was always observed either under photosynthetic or dark-respiratory conditions. Thus, parallel variation appears to be a common character of the adjustments of photosystem stoichiometry. This evidence leads us to think that the electron turnover capacity of the two terminals in thylakoid ETS is regulated by a similar mechanism, at least in *Synechocystis* PCC6714. However, how is Cyt *c* oxidase activity regulated, through *de novo* syn-

thesis like PS I, or through the activation-deactivation of existing enzymes?

Is variation of photosystem stoichiometry common in oxygenic photosynthesis?

As noted above and reviewed by Anderson (1986, see also Table 1), the photosystem stoichiometry in vascular plants also varies in response to light intensity, and the mode of variation appears to be the same as that in cyanophytes. Further, the variation in response to light quality (Kim et al. 1993) for maintaining the photosynthetic efficiency (Chow et al. 1990) has been also reported. Recently, we observed the variation of the same type in the green alga *Chlamydomonas reinhardtii* (Melis et al. 1996) where the variable component appeared to be PS I. Further, the variation seemed to be primarily induced by changes in the synthesis, but not the degradation, of PS I (Murakami et al. 1997b). Since the variation was also observed with red algae (Cunningham et al. 1990; Abe et al.1993), the ability for the regulation of the photosystem stoichiometry seems to be common in algae and plants in the green and red phylogenetic lineage. However, no positive evidence has thus far been observed with yellow plants such as diatom. We have also failed to observe PS I/PS II variation in the diatoms *Chaetocerus socialis* and *Skeletonema costatum* and thus wonder if the photosynthetic system in yellow plants lacks the ability to adjust. It is also possible that studies on the photosynthetic apparatus in yellow plants have not been concentrated on the variation of photosystem stoichiometry, and that this phenomenon may have been ignored.

Conclusion

Our studies have provided a rough sketch of the regulation of the photosystems in response to changing the light regime. How the regulatory mechanism works is still under speculation. Limitation of our study is more or less ascribed to our attitude toward research, since we have persisted in using physiological techniques. Elucidation of molecular mechanism must await analyses with more biochemical as well as molecular biological techniques. Such modern techniques will markedly accelerate the progress of the study. New knowledge at the molecular level is rapidly accumulating and will allow us to give better understanding of the mechanism at work. New knowledge may revise our model of some parts, or redraw a completely different one. Whichever it is, I am watching, with a great expectation, for a real mechanism that will be brought to light in the near future.

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